THE COMPARATIVE ANATOMY AND PHYLOGENY OF THE CASUARINACEAE

BY

MAYNARD FOWLE MOSELEY, JR.

B. S., University of Massachusetts, 1940

M. S., University of Illinois, 1942

AN ABSTRACT OF A THESIS

SUBMITTED IN PARTIAL FULFILLMENT OF THE REQUIREMENTS
FOR THE DEGREE OF DOCTOR OF PHILOSOPHY IN BOTANY
IN THE GRADUATE SCHOOL OF THE
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R. UNIV. BIBLIOTHEEK LEIDEN

THE COMPARATIVE ANATOMY AND PHYLOGENY OF THE CASUARINACEAE

Most of the phylogenetic systems of the Angiosperms in use today are based chiefly on the morphology of the flower; yet, there is a growing conviction among botanists that a natural classification of the plant kingdom must be founded on the combined evidence taken from all the fields of botanical endeavor. Thus during the last three decades or so, there has been a serious attempt to use the available data derived from taxonomy, anatomy, cytology, palaeobotany, and other fields of research to construct phylogenetic systems of classification.

Plant anatomists have established, by methods independent of any system of phylogeny, lines of phylogenetic specialization of the stele, particularly of the secondary xylem. These lines of specialization in the evolution of the imperforate tracheary elements, vessel elements, vascular rays, wood parenchyma cells, and other structures of the secondary xylem are used by the wood anatomist to trace the phylogeny of families and orders of the Angiospermae. Following this, the anatomist attempts to harmonize his results with whatever evidence is available from other fields of study.

Because of the promise extended by the "anatomical method", this investigation (largely of the secondary xylem), was undertaken to contribute toward a better understanding of the evolutionary status of the Casuarinaceae (one genus, *Casuarina*). An attempt is made to harmonize the anatomical data first with the evidence suggested by the various phylogenetic systems based mostly on floral morphology, and then with the available facts offered by the fields of phloem anatomy, embryology, nodal anatomy, cytology, palaeobotany, and ecology.

As a result of the original investigation, a thorough

anatomical description of the family is presented, the outstanding anatomical characteristics of the species or groups of species are listed, and the anatomical variation within certain species is described. An anatomical analysis of Bentham's and of Poisson's taxonomical studies is attempted. A brief survey of the secondary phloem is also given.

Slides of the secondary xylem of both old wood (at some distance from the pith) and young wood (relatively close to the pith) of one hundred and seventy specimens were examined. Ten slides were made of each specimen, two unstained and eight stained. This study involved the investigation of twenty-nine species of *Casuarina*.

The direct results of the anatomical study of the secondary xylem are several and these will be described as succinctly as possible.

1. The anatomical description of the genus may be summarized as follows: Growth rings are poorly defined or absent; both tracheids and fiber-tracheids are found in all but one species, where only tracheids occur; tracheids generally predominate and the larger, thinner-walled tracheids are vasicentric; the fiber-tracheids often have very thick walls; the fibrous elements are extremely short to moderately long, mostly short to medium-sized; spiral thickenings occur in the fibrous elements of six species.

The range of species means for the number of vessels per square millimeter is from moderately few to very numerous; vessel distribution is universally solitary; diffuse-porosity is characteristic, although there is a very slight tendency toward ring-porosity; the majority of species have vessel elements which are thin-walled, and circular in outline, although thick-walled, circular to angular vessels occur in seven species. Vessel diameters range from very small to moderately large (genus mean is 63 u, or moderately small), mostly from very small to medium-sized.

The old wood of eight species has vessel elements with

only simple perforation plates, the remaining species have scalariform and simple perforation plates. Among the species with scalariform plates, the majority have plates with the intermediate number of bars; the bars of the scalariform plates are completely bordered, and the openings between the bars are predominantly narrow. Most species have vessel elements with sloping end walls, most frequently from 40° to 80°; transverse end walls are not uncommon in some species, however. Intervascular and ray-vessel pitting is largely alternate. The range of vessel element lengths fall in the very short to moderately long classes; the genus mean is 439 u (medium-sized). Spiral thickenings occur characteristically in the vessel elements of thirteen species, and sporadically in five species; the remaining species have vessel elements with generally no spiral thickenings.

The vascular rays are heterogeneous II B. Aggregate rays occur in the old wood of twenty-three species, but are absent in four species. Metatracheal parenchyma occurs in all species, diffuse in nearly all, and the paratracheal types in one.

2. The taxonomic divisions of the genus by Bentham and by Poisson are considered on an anatomical basis. In general, the anatomical evidence supports the respective divisions of the genus, but it is suggested that *C. torulosa* and *C. decaisneana* might better be placed in *Leiopitys*. Anatomical characters are used to assign to sections, species given binomials since the time of Bentham, and later of Poisson. Suggestions are offered, based on anatomical data, for a better understanding of certain species. A survey of the present taxonomical status of the genus reveals that a taxonomic monograph would be extremely valuable.

3. Anatomical descriptions of the individual species, or occasionally groups of species, are given. In most cases, combinations of anatomical characters distinguish the species. There is often considerable variation in the anatomical characteristics within a species.

4. The aggregate ray in *Casuarina* is considered to arise in ontogeny and to have arisen in phylogeny by the aggregation of uniseriate and multiseriate rays. Generally, compound rays (found in a few species) arise from aggregate rays. The aggregate and compound rays undergo dissection to some extent in the later development of the xylem in all the species.

By a careful interpretation of the anatomical data obtained from this investigation, and by a comparison of the anatomical evidence with that offered by floral morphology, the author has reached certain conclusions concerning the phylogenetic relationships of the Casuarinaceae. These conclusions are as follows:

1. On anatomical evidence, it is concluded that the Casuarinaceae are a specialized family of the Angiospermae and are not a primitive one. The evidence also indicates that the specialization is, however, moderately advanced rather than highly advanced.

2. Floral morphology indicates that the Casuarinaceae have been derived from hamamelidaceae-like ancestors. The lines of floral reduction seen in the Hamamelidaceae seem to have been carried to extremes in the Casuarinaceae.

3. A study of the correlation between flower structure and anatomy of the Casuarinaceae precludes the retention of the family as a primitive group (or the primitive group) of the Angiospermae. In addition, the anatomical evidence presented supports, or at least is not inconsistent with, the derivation of the Casuarinaceae from hamamelidaceous-like ancestors as suggested by floral morphology.

The additional lines of evidence offered by the available data from other fields of botany were found to suggest no serious inconsistencies with the phylogenetic conclusions stated above. The conclusions from the other lines of evidence are:

1. The secondary phloem is moderately advanced. The outstanding sclerification of ray cells and the production of

large stone cells indicate specialization. The sieve-tube elements are of the second type—with moderately oblique end walls, and with a non-functional lattice-work on the side walls—and denote a moderate specialization relatively equal to the evolutionary level attained by the xylem. This moderate advancement supports the conclusions based on wood anatomy and floral morphology.

2. The numerous gametophytic abberations of *Casuarina* are discussed, and the conclusion is reached that these atypical characters are sporadic peculiarities which have little if any phylogenetic significance. It is noted that the embryo-sac and the embryo of *Casuarina* are typically angiospermous.

3. As the foliar supply in *Casuarina* is composed of one vascular strand which forms one gap in the central stele, the nodal anatomy also offers evidence in favor of the non-primitiveness of the family and of the derivation from the trilacunar Hamamelidaceae.

4. The recorded chromosome numbers of *Casuarina*—8, 9, and 12—could have been derived from the hamamelidaceous basic number of 12 by the methods suggested by Wanscher.

5. The paucity of authenticated fossil *Casuarina* specimens offers little assistance to the problem of phylogeny; but, if anything, the lack or scarcity of early specimens lends support to the thesis that the Casuarinaceae are derived and are of relatively recent origin.

6. It is thought that the characters of *Casuarina* (often considered as simple and thus linking the Gymnosperms and Angiosperms, but considered in this investigation as reduced) are due in part, at least, to the xeric conditions under which most of the species exist. The fact that most of the species of *Casuarina* grow in soils that are either physiologically or climatically arid, suggests that the resemblance of *Casuarina* to the similarly xeric *Ephedra, Pinus,* and *Equisetum* is a result of convergent evolution .

VITA

The author was born in Boston, Massachusetts, on July 15, 1918. He received his elementary training in the Boston Public Schools, Boston, Massachusetts. He was graduated from the Jamaica Plain High School, Boston, in 1935. During the years of 1936-1940, he attended the University of Massachusetts at Amherst, Massachusetts, and received the B. S. degree with a major in Botany in June, 1940. During the academic years of 1940-1942, he carried on graduate study in Botany with a minor in Zoology while serving as an Assistant in Botany at the University of Illinois. He received the M. S. degree in Botany from the University in June, 1942. His M. S. thesis was published in 1943 under the title of "Contributions to the life history, morphology, and phylogeny of *Widdringtonia cupressoides*" in Lloydia 6: 109-132. He entered military service with the Army of the United States in December, 1942, and during most of the war served with the 297th General Hospital as a clinical laboratory technician. He saw foreign duty in the European Theater of Operations from June, 1944, to August, 1945. The writer returned to the University of Illinois in March, 1946, as a graduate student and Assistant in Botany. He was granted a Fellowship in Botany for the academic year 1946-1947. The author is a member of the Botanical Society of America, the American Association for the Advancement of Science, and of the Sigma Xi and Phi Kappa Phi honorary societies. He has been appointed an Instructor in Botany at Cornell University for the coming year.